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Object manipulation and tool use in Nicobar long-tailed macaques (Macaca fascicularis umbrosus)

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Abstract:	Object manipulation and tool use by non-human primates have received considerable attention from primatologists and anthropologists, because of their broad implications for understanding the evolution of tool use in humans. To date, however, most of the studies on this topic have focused on apes, given their close evolutionary relationship with humans. In contrast, fewer studies on tool use and object manipulation have been conducted on monkeys. Documenting and studying object manipulation and tool use in species that are more distantly related to humans can provide a broader perspective on the evolutionary origins of this behaviour. We present a detailed description of tool-aided behaviours and object manipulation by Nicobar long-tailed macaques (Macaca fascicularis umbrosus) living along the coastlines of Great Nicobar Island. We made observations from December 2018 to March 2019, using ad libitum and focal sampling methods. We observed behaviours related to object manipulation and tool use in six different behavioural contexts (foraging, hygiene, communication, play, self-directed and self-hygiene behaviour) involving eight different types of objects, namely resonance rod, play object, rolling platform, scraping tool, dental groom, pounding substrate, leaves as grip pads and wipers, and stimulation tool. We observed that males were involved in tool use and object manipulation more frequently than females. Our results add to existing records of object manipulation, tool-use behaviour and tool variants displayed by non-human primates, showing that Nicobar macaques perform multiple and diverse tool-aided behaviours.

Title **Object manipulation and tool use in Nicobar long-tailed macaques (*Macaca fascicularis umbrosus*)**

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CONFLICT OF INTEREST- During any phase of this study and article preparation there no potential conflict of interest has been reported.

ETHICAL ISSUES AND PERMISSION – The present study was approved by IISER, Mohali Research Committee and the permit (No.CWLW/WL/134/332) was issued by the Andaman and Nicobar Forest Department, India. The present study has abided by all the guidelines set forth by the Government of India, Andaman and Nicobar Island territory Forest department. Further, the data obtained during the present study were purely observational and have followed the best practice on field primatology set forth by the International Primatological Society.

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ABSTRACT

Object manipulation and tool use by non-human primates have received considerable attention from primatologists and anthropologists, because of their broad implications for understanding the evolution of tool use in humans. To date, however, most of the studies on this topic have focused on apes, given their close evolutionary relationship with humans. In contrast, fewer studies on tool use and object manipulation have been conducted on monkeys. Documenting and studying object manipulation and tool use in species that are more distantly related to humans can provide a broader perspective on the evolutionary origins of this behaviour. We present a detailed description of tool-aided behaviours and object manipulation by Nicobar long-tailed macaques (*Macaca fascicularis umbrosus*) living along the coastlines of Great Nicobar Island. We made observations from December 2018 to March 2019, using *ad libitum* and focal sampling methods. We observed behaviours related to object manipulation and tool use in six different behavioural contexts (foraging, hygiene, communication, play, self-directed and self-hygiene behaviour) involving eight different types of objects, namely resonance rod, play object, rolling platform, scraping tool, dental groom, pounding substrate, leaves as grip pads and wipers, and stimulation tool. We observed that males were involved in tool use and object manipulation more frequently than females. Our results add to existing records of object manipulation, tool-use behaviour and tool variants displayed by non-human primates, showing that Nicobar macaques perform multiple and diverse tool-aided behaviours.

KEYWORDS – Great Nicobar Island, forage, self-hygiene, play, self-directed, sex-bias, behaviour plasticity

INTRODUCTION

Tool use is commonly defined as the use of a freely movable object (the "tool") with the goal of either altering the environment, another object or organism, or mediating the flow of information between the user and the environment or between the user and other organisms (Beck 1980; Shumaker et al. 2011; St Amant and Horton 2008). Tool use by non-human primates has received a great deal of attention due to the close evolutionary relationship with humans (Haslam et al. 2009). Studying tool-associated behaviours in primates has helped us understand the diverse range of behavioural patterns across primate species, providing valuable information on the evolution of tool use in the hominin lineage (King 1986; Pal et al. 2017). Most of these studies have been conducted on the great apes (Arroyo et al. 2016; Breuer et al. 2005; Call and Tomasello 1994; Estienne et al. 2019; Fontaine et al. 1995; Gross 2005; Gruber et al. 2010; Kahlenberg and Wrangham 2010; Kaplan 2009; Pascual-Garrido 2019), while comparatively fewer studies have been conducted on monkeys such as capuchins (genus *Sapajus*) and long-tailed macaques (*Macaca fascicularis*) (Haslam et al. 2009, 2017; Ottoni and Izar 2008). Variation in tool use has been described both between and within species and across different geographical regions. West African chimpanzees (*Pan troglodytes verus*), for example, use stones to crack nuts, whereas this behaviour is absent in East African chimpanzees (*Pan troglodytes schweinfurthii*) (Whiten et al. 1999), while tools used for termite fishing vary between the neighbouring communities of chimpanzees in Gombe, Tanzania (Pascual-Garrido 2019). Similarly, long-tailed macaques on the eastern side of the Andaman sea (i.e., in Thailand) use stone tools for percussion on oysters (Malaivijitnond et al. 2007), whereas the use of stone tools appears to be absent in the macaque population on the western side of the Andaman sea (i.e., in India) (Pal et al. 2017). These intra-specific differences in tool use are intriguing and raise the question of the ecological conditions that might lead different populations of the same species to vary in tool-use behaviours.

Tool use among non-human primates has been related to six different activities: defence, hunting, social display, hygiene, food extraction and aggression (Sanz et al. 2013; Shumaker et al. 2011; van Schaik et al. 1999). However, most observations of tool use in monkeys and apes are associated with foraging behaviour (Allritz et al. 2013; Haslam 2018; Haslam et al. 2017; Sanz et al. 2013; Tan et al. 2015; Whiten et al. 1999). Fewer studies have investigated tool use in non-foraging contexts, and this work has largely been conducted on apes and capuchins (Falótico et al. 2017; Luncz et al. 2017; Luncz et al. 2017; Meulman and Van Schaik 2013; Westergaard et al. 1998; Whiten et al. 1999). Although the need to access otherwise inaccessible food items was probably one of the main driving forces leading to the adoption of tools in the hominin lineage, evidence suggests that extinct hominins expanded the use of tools to a variety of non-foraging contexts (Boyd and Silk 2009). Therefore, it is essential to understand tool use in non-foraging context as this can provide a broader perspective on the factors that might have affected the evolution of tool use in humans.

While there is an abundance of reports of tool use among non-human primates, cases of simpler object manipulations are more rarely reported (e.g., stone handling in Japanese macaques, *Macaca fuscata*: Huffman and Quiatt 1986). However, observing and understanding how animals manipulate objects can shed new light on how tool use may arise. Accumulating evidence suggests that object manipulation enhances individuals' familiarity with them, increasing the probability of the employment of these objects as tools (Beck 1980; Menzel Jr et al. 1970). Among West African chimpanzees, for example, the offspring of females who engage in nut-cracking behaviour are more exposed to a variety of stones which they manipulate and use to practice their nut-cracking skills. Recent evidence suggests that such exposure to the stone tools and the possibility of playing with them increases the immatures' chances of mastering nut-cracking in adulthood (Estienne et al. 2019). Among Japanese macaques, some juveniles who engaged in stone handling while playing developed the ability

to use stones as tools in the feeding context in adulthood (Huffmann and Quiatt 1986). Similarly, among bonnet macaques (*Macaca radiata*), individuals living in an urban environment who were more exposed to novel objects in their surroundings were better at experimentally extracting food from a bottle than individuals living in natural conditions (Mangalam et al. 2013). Collectively, these studies show that studying object manipulation can provide crucial information on the ecological, social and cognitive conditions in which tool use might arise.

Long-tailed macaques are an excellent model to study object manipulation and tool use, as previous work has shown that this macaque species uses tools for personal hygiene (i.e., use of hair as dental floss), as stimulus provider (i.e., use of sticks for erotic stimulation) (Sinha 1997; Watanabe et al. 2007), and in foraging contexts (Carpenter 1887; Hohmann 1988; Luncz et al. 2017; Malaivijitnond et al. 2007; Pal et al. 2017; Proffitt et al. 2018).

Long-tailed macaques have a wide distribution in Southeast Asia, but in India they are found only in the Nicobar islands, with approximately 79 groups scattered across three islands with varied ecological terrains (hilly, rain forest ecosystem, rocky landform) (Sivakumar 2010; Velankar et al. 2016). The 2004 tsunami resulted in a sharp decline in Nicobar long-tailed macaques' coastal area population (Sivakumar 2010), and this population is now listed in Schedule I, Part I, Indian Wildlife Protection Act, 1972. This species' s ability to adapt to different ecological conditions makes them a suitable model for understanding primate adaptation (Luncz et al. 2017). We aimed to document tool use and object manipulation in the long-tailed macaques living in the Nicobar islands. We describe the object manipulating and tool-aided behavioural patterns recorded during four months of observations of macaques living near the coastal areas in the Great Nicobar Island.

METHODS

Study site and subjects

We collected data from one Nicobar long-tailed macaque group, named BQ group (Fig.1) between December 2018 and March 2019 at Campbell Bay in Great Nicobar island of the Andaman and Nicobar Island Territory, India (Fig. 1). We conducted an initial survey to identify members of the group, mostly when the macaques moved out of the forest region. Based on the survey, we identified 28-43 individuals, including 4-8 males, 5-8 females, 5-11 subadults, 5-13 juveniles and 0-4 infants. The movement of this group during the study was restricted to between 7° 1'6.35"N and 7° 0'35.47"N latitude and between 93°56'2.36"E and 93°56'13.88"E longitude. The island had several habitats, including hilly landscapes, rainforest cover, sandy beaches and artificial (human-made) gardens. During the study, the macaques foraged on coconuts (*Cocos* sp.) and screw-pine trees (*Pandanus* sp.) near the beach and from gardens near the human settlement, which was 120 m from the beach. We also observed them foraging on mangos, guava, insects, and *Casuarina* sp. plants. The macaques were very habituated to human presence.

Behaviour data collection

We collected data between 04:00-13:00 h and 14:30-17:00 h using a combination of *ad libitum* and focal animal sampling (Altmann 1974; Huffman and Quiatt 1986; Mallapur et al. 2005). Initially, we took *ad libitum* notes to record the macaques' behaviour. These initial observations showed that 14 individuals used tools and manipulated objects. We identified these individuals on the basis of their facial features, scars and age class. Subsequently, we used focal animal sampling on these 14 individuals to document their behaviour systematically. In three instances of object manipulation (i.e., during rod shaking), we could not clearly identify some of the subadults, so we did not include these individuals in the list of focal subjects.

We collected data via 15-min focal animal samples using HanDBase software (Version 4.1.5d) (Altmann 1974). When we could see more than one focal subject, we randomised the

sampling order, by generating a random list and selecting the focal subject on the basis of the order in which they appeared in the list. When only one subject was visible, we sampled this subject, then searched for other focal subjects. During focal animal sampling, we recorded the following information: 1) the types and number of tools and objects manipulated; 2) the context in which the behaviour took place; 3) the number and identity of other individuals performing the same behaviour; and 4) the sequence of behaviours associated with the tool-aided behaviour or object manipulation. If the tool use or object manipulation continued for more than 15 minutes, we continued recording the behaviour until it ended. Although this approach may potentially bias some of our data, our primary goal was to provide a description of tool-use behaviours and object manipulations that was as complete and accurate as possible.

Ethical notes

The study was approved by IISER, Mohali Research Committee and the permit (No. CWLW/WL/134/332) was issued by the Andaman and Nicobar Forest Department, India. The study complied with all the guidelines set forth by the Government of India, Andaman and Nicobar Island territory Forest department. The study was purely observational and followed the best practices of field primatology set forth by the International Primatological Society.

Data availability statement

The data collected during the current study are available from the corresponding author on reasonable request.

RESULTS

We observed 14 individuals: 7 adult males, 2 adult females, 2 subadults and 3 juveniles. We recorded 33 cases of tool use or object manipulation in six behavioural contexts: foraging (i.e., food processing), hygiene, self-directed behaviour, self-hygiene, play and communication (Fig. 2; Table 1). The macaques manipulated eight types of objects: rolling and pounding substrate,

148 scraping tool, leaves as grip pad and wiper, stimulation tool, dental groom, play tool, and
149 resonance rod (Fig. 3).

150 **Stone or wood as a pounding substrate**

151 We observed macaques carrying mature coconuts to hard surfaces like stone or wood, and
152 pounding the coconut against the substrate (Fig. 4; supplementary video). We termed the hard
153 surface used for percussion the pounding substrate (Haslam et al. 2019). Macaques used two
154 types of pounding substrate: natural (rocks and tree branches) and artificial (roads and wooden
155 railings). The number of strikes varied between individuals, and may be related to the hardness
156 of the food. We only observed males using pounding substrates to break open mature coconuts.
157 We observed four cases of stone substrates and two cases of wooden substrates, all of which
158 were used to break mature coconuts.
159 Macaques changed pounding substrate to use a more appropriate surface. In one case, for
160 example, a macaque started with one stone substrate, then switched to another stone substrate
161 (Fig. 5). On closer observation, the first substrate was softer and irregular than the second
162 substrate, and was surrounded by many broken pieces of stone. The second pounding substrate
163 had fewer scar marks and breakage and was more durable than the first substrate. Therefore,
164 the second substrate was likely to be more suitable than the first one as a pounding substrate
165 because of its durability, shape and size.

166 We also observed macaques change the technique they used to process food. Some first
167 pounded the coconut on the substrate, then rolled the coconut on the ground while holding it
168 with leaves. In three cases, after an individual abandoned a coconut, another individual
169 collected it and tried to open it by rolling it on the substrate in the same way as the first
170 individual. Occasionally, the new individual tried to open the coconut in a different way to the
171 previous individuals by, for example, probing the fruit with their fingers near the functional

pore then rolling the coconut on the ground, holding it with a leaf. In one case we observed the macaque pound the coconut against the substrate, then roll it on the ground, then pound it on the substrate again. In another case, the individual also tried to process the coconut using a wooden substrate, by pounding it against the hard surface and probing the functional pore with their fingers. The macaque then licked his fingers and repeated the action.

Log as a rolling substrate

We observed three cases of macaques rolling food on horizontal tree trunks or logs (Fig 6; supplementary video). All three cases involved adult males, who rolled decomposed coconut and the phloem (i.e., the part of a tree below the bark) from dry wooden logs. The macaque rolled the food item back and forth on the log by pressing it with his palm, then consumed the food. If the food item was a decomposed coconut, the macaque occasionally probed the functional pore of the coconut with his finger, licked his fingers and repeated the rolling and probing behaviour. Rolling the food in this manner pushed the flesh of the decomposed coconut closer to the functional pore of the fruit, allowing the macaque to extract the coconut with its fingers. Macaques used different plant species as a rolling substrate, but in all cases the surfaces appeared to be functionally suitable. The macaques seemed to select logs with an even or smooth surface and which were large enough to roll the food on. Our observations suggest that macaques tended to use the "rolling" technique for decomposed coconuts, and the "pounding" technique for coconuts that were fresh and newly ripened.

Sticks as a scraping tool

One adult male displayed this behaviour on three occasions (Fig. 7; supplementary video). The macaque took either a dry leaf or a fresh thin stick of *Casuarina* sp., then picked up another small twig. In all three cases, he held the twig in his right hand and the leaf/stick in his left hand. He kept the twig straight and moved it towards his left hand and pulled the leaf/stick by

holding it against the twig and pressing it with his right thumb. This smoothed the surface of the leaf/stick, which the macaque then ate. In one case, the twig fell from his hand, and the macaque picked it up and continued the behaviour. On one occasion a subadult male sitting close by observed the male performing the behaviour. Later, we observed the subadult performing the same behaviour but he was not successful, as he could not orient the stick in a manner that enabled free movement of the leaf/ stick against the twig.

Leaves as grip pad or as wipers

We recorded six cases of the use of leaves as tools (Fig. 8; supplementary video). Macaques used leaves four times as a "grip pad" to hold food while they processed it, and twice as "wiper", possibly to clean the food. We also observed the macaques uprooting small plants to use as a firm grip while processing food. All cases involved mature coconuts as food items. The macaques held coconuts using the leaf, then shook or rolled the fruits vigorously at intervals. In between, the macaque shook the coconut, probed it with his fingers and licked the endosperm which came closer to the functional pore of the coconut. Macaques also placed the coconut on a leaf as they rolled it and licked the leaf to obtain endosperm that leaked onto it. If the leaf slipped from the macaque's hands, he picked it up immediately and continued with the behaviour.

Stimulation stick

We observed this behaviour once in one adult male (Fig. 9). The macaque picked up a long stick and removed its twigs to make it uniform. Then, he used the stick to rub/ scratch his genital area vigorously. He made a total of 12 strokes (1 stroke = one complete up and down hand movement with the stick), then discarded the stick. He may have used the tool to scratch an irritation or to provide erotic stimulus, but it was difficult to understand the purpose of this behaviour as we only saw it once.

220 **Fibres for dental grooming**

221 Two adult females performed this behaviour. When the individuals came across a nylon or
222 coconut fibre rope, they took the threads out of the rope and selected a fine string, which they
223 placed between their teeth using one or both hands. Next, the macaques pulled the string out
224 of their mouth, then investigated the string. We also observed the macaques picking particles
225 off the string and eating them. This behaviour looked, therefore, more like 'teeth picking' (i.e.,
226 placing a fibre or object between the teeth and pulling it outwards, then investigating the fibre
227 or object and consuming food particles that might have got stuck in the teeth and then become
228 attached to the fibre while flossing) than flossing (i.e., placing a fibre or object between the
229 teeth and pulling it outwards, without investigating the fibre or object afterwards).

230 **Stick for play**

231 This type of object manipulation was restricted to three juveniles (Fig. 10). We recorded five
232 cases of juveniles carrying branches and dragging them around. Once, one juvenile passed a
233 branch to another juvenile who then dragged it along. The macaques carried the branches for
234 47 seconds to an hour, during which they walked, climbed, jumped, rested, slept and foraged
235 while holding the branch.

236 **Resonance rod for communication**

237 We observed the macaques shaking the iron rods of an unfinished building rhythmically on
238 seven occasions (Fig. 11; supplementary video). Only one individual performed this behaviour
239 at any given time, while other individuals observed, then performed the same behaviour in a
240 similar or different pattern. We observed the macaques rod shaking in two contexts, either
241 when moving out of the forest, or during an aggressive display. Of the five adult males and
242 unidentified subadults who showed this behaviour, we saw three adult males use a resonance
243 rod in both contexts.

We observed rod shaking twice when the macaques were moving out of the forest. In this context, three adult males shook the rods one after the other when the group reached the edge of the forest in the morning. We suggest that macaques might have performed this behaviour to communicate with the other group members and coordinate their group movement when moving out of the forest. In this context, the rhythmic sound produced by the shaking of rods was similar across the individuals who made it, suggesting that subsequent individuals tried to replicate the pattern and number of rod shaking instances displayed by earlier individuals, producing the same rhythmic sound. For example: in one case, the first individual shook a rod three times before moving away, followed by second male who also shook the rod three times, and the third individual also did the same.

We observed rod shaking in an aggressive context on five occasions involving five adult males and some unidentified subadults. We observed adult males displaying this behaviour twice: the first time, three individuals were involved (two males against one male) while the second time five males were involved (four males against one male). We also observed unidentified subadults rod shaking in an aggressive context three times. In this context, the individuals shook the rod in a different patterns/ rhythms, and the shaking became more vigorous with each individual who performed it. The individuals shook the rods and made vocal threats, one at a time, repeating the display multiple times, until one of the individuals involved moved away. This behaviour resembles branch-shaking behaviour, which is a prevalent form of aggressive behaviour among macaques (Milich and Maestripieri 2016). Thus, the macaques might have selected a new object (i.e., iron rods) to display their aggression, creating a louder noise, helping the individual to sound like a substantially larger or stronger individual.

DISCUSSION

We report six types of object manipulation and tool use in Nicobar long-tailed macaques, adding new data to the records of tool behaviour and object manipulation by Old World monkeys. Our observations show that Nicobar long-tailed macaques use substrates to process food (by pounding or rolling food items on the ground or wooden logs), employ leaves as wipers or grip pads to clean or manipulate food items, use sticks to scrape food or scratch themselves, and use resonance rods for social display or communication. Some of the objects described in this study fall into the category of "tool", following the definitions of tool use by St Amant & Horton (2008) and Shumaker et al. (2011). The strings used as "toothpicks/ floss" and the sticks used to scratch the genitals, for example, are movable objects used to alter the organism performing the behaviour (by removing food remains from the teeth or reducing body irritation). Similarly, the use of leaves as wipers can be classified as "tool use" since leaves are used to modify the environment. Similar types of tools have been described in this and other species. For example, Nicobar long-tailed macaques have been described to use leaves to wrap food items, and to use sticks for dental floss (Pal et al. 2017). The use of sticks for scratching and of leaves as wipers have also been reported in both bonnet macaques (Sinha, 1997) and orangutans (*Pongo* sp.) (Meulman and van Schaik 2013). Although the other cases of object manipulation we observed do not fall into the "tool use" category because the object used is not movable (e.g., the resonance rod used for social or aggressive display or the log used for rolling food items on it), they shed new light on macaque cognitive abilities. The use of different substrates and techniques to open coconuts, for example, likely requires prior knowledge of the material and the strategies needed to open the hard shell, suggesting high levels of cognitive skills. Future studies should examine whether macaques consistently use the same substrates and logs to process the food items, which would indicate advanced cognitive and sensorimotor intelligence, in the form of excellent memory, ability to plan and the capacity to mentally map their territory.

There are many similarities but also large differences in the types of tools used and objects manipulated in different long-tailed macaque populations. Similar to our study population, Thai long-tailed macaques, for example, use objects as dental floss, with the only difference being that Thai macaques use human hair rather than nylon or coconut fibres (Watanabe et al. 2007). Furthermore, both Burmese and Nicobar long-tailed macaques use complex manipulative skills to process food items and facilitate consumption (Tan et al. 2016; Pal et al. 2017). However, some behaviours appear to be population-specific. Burmese macaques, for example, use stones to open molluscs and nuts (Falótico et al. 2017; Gumert et al. 2009; Malaivijitnond et al. 2007), while no other long-tailed macaque population has been described to use stone tools to our knowledge. Similarly, Nicobar long-tailed macaques are the only macaque population that has been described to pound coconuts on a hard surface to open the fruit. Such variability is likely to be partially explained by differences in ecological conditions. On Great Nicobar island, for example, there seems to be a scarcity of large rocks that could be used as tools, which might explain why the use of stone tools has not emerged in this population. Other populations of long-tailed macaques, such as those living in Bali, feed on coconuts (Wheatley 1988), but these populations remove the outer fibrous skin and either drink the coconut water or scoop the endosperm out with their hands and eat it, and they have never been observed pounding the coconuts on a hard surface to break them open. This raises the intriguing possibility that ecological conditions might not be enough to explain differences in food extraction techniques between macaque populations. Similarly, studies of chimpanzees and orangutans (*Pongo* sp.) have shown that differences in habitat are not enough to explain behavioural variations across populations (Whiten et al. 1999; van Schaik et al. 2003).

It is possible that some of the population-specific traditions in long-tailed macaques originated from a handful of particularly skilful and innovative individuals who were the first to come up with a solution to open coconut shells. These solutions might have then been passed

317 on to future generations through social learning. Although our observations cannot provide
318 conclusive evidence that the behaviours described in the present study are socially learned, we
319 frequently observed macaques watching other individuals manipulating an object, and
320 occasionally trying to replicate the behaviour, as in the case of the use of sticks as scraping
321 tool.

322 After decades of observations, only two individuals among the rhesus macaques
323 (*Macaca mulatta*) on Cayo Santiago have been observed pounding coconuts to open them
324 (Visalberghi and Fragaszy 1990). Visalberghi and Fragaszy (1990) suggest that the behaviour
325 has not spread in the population because the action needed to open the coconut is too
326 complicated to learn by watching alone. It is possible, however, that motivation plays a key
327 role in the learning process. Macaques on Cayo Santiago are provisioned daily with monkey
328 chow and commercial feed, while the lack of good alternative sources of energy might have
329 increased the motivation to learn coconut pounding among the Nicobar macaques.
330 Furthermore, rhesus macaques are more despotic and less tolerant than long-tailed macaques
331 (Thierry et al. 2004), which decreases the ability of subordinates to monopolize resources. For
332 example, one of the two male macaques who pounded coconuts among the Cayo Santiago
333 rhesus macaques soon stopped the behaviour after more dominant individuals began stealing
334 the coconut meat from him (Visalberghi and Fragaszy 1990). In contrast, we never observed
335 dominant Nicobar macaques stealing coconut meat from subordinates. Some of the behaviours
336 we describe, such as the use of sticks as scraping tools or to scratch specific body regions, were
337 performed by only one individual. It will be important to continue monitoring this macaque
338 population as this could reveal whether, how, and to what extent, these behaviours spread
339 through the population.

340 Our observations suggest that the skills required to manipulate objects among long-
341 tailed macaques might emerge early in life, as juveniles commonly use sticks as toys. This

342 early emergence of manipulative skills resembles studies conducted in other populations of
343 long-tailed macaques and in other primate species that commonly use tools. For example, in
344 Thai long-tailed macaques the ability and propensity to manipulate objects begin in the first
345 three months of life (Tan 2017). Similarly, juvenile chimpanzees and bonobos use sticks during
346 social play (Gruber et al. 2010) or as "dolls" (Kahlenberg and Wrangham 2010), while the
347 stone handling behaviour displayed by Japanese macaques during infancy increases
348 individuals' ability to use stones as tools in adulthood (Huffman and Quiatt 1986). Future work
349 on the Nicobar long-tailed macaques will shed light on the ontogeny of object manipulation
350 and tool use, and to what extent other group members influence the learning process.

351 Finally, one of the most striking characteristics of object manipulation and tool use
352 among Nicobar long-tailed macaques is the strong sex bias, as the majority of the tools were
353 used by adult males. For at least some of the behaviours reported in our study, it is very likely
354 that the sex bias in object manipulation is related to the size and weight of the object that needs
355 to be manipulated. Coconuts can be very heavy for macaques and males might manipulate them
356 to successfully pound or roll them on a surface more easily than females given their bigger
357 body mass. Similar sex biases in tool use have been described in other long-tailed macaque
358 populations (Gumert et al. 2011) and in capuchin monkeys (Barrett et al. 2018; Falótico and
359 Ottoni 2014; Spagnoletti et al. 2011), in which males are more likely to use heavy stones to
360 crack the hard shells of food items than females.

361 Our findings add information on the tool-use and object-manipulation skills of Nicobar
362 long-tailed macaque population. The study paves the way for a more detailed investigation of
363 the factors influencing tool manufacture and use across macaque groups that could help to
364 understand the geographical clustering of tool technology across species. Furthermore, the
365 different behaviours associated with tool use in Nicobar long-tailed macaques could open up
366 avenues for understanding models of social learning. There are several differences in tool-use

and object manipulation abilities between this long-tailed population and other populations found outside India (i.e., in Thailand or Burma) in both feeding and non-feeding contexts (Malaivijitnond et al. 2007; Watanabe et al. 2007; Pal et al. 2017). More work is needed to better understand the social, demographic and ecological factors which influence tool-use and object manipulating behaviour in this and other species. Comparative work across different long-tailed macaque populations can shed new light on the evolution of tool culture and technologies and the factors that affect the emergence of tool-use abilities.

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532 **Figure Legend**
533 Fig. 1 Location of the field site (© *Google Earth*)

Fig. 2 Frequency of tools and objects used and associated behaviour displayed by Nicobar long-tailed macaques at Campbell Bay, Great Nicobar island, India, December 2018 to March 2019.

Fig. 3 Number of Nicobar long-tailed macaques of each age/sex class observed using tools and objects at Campbell Bay, Great Nicobar island, India, December 2018 to March 2019.

Fig. 4 Use of different pounding substrates by Nicobar long-tailed macaques at Campbell Bay, Great Nicobar island, India, December 2018 to March 2019. These pounding substrates were either artificial, such as wooden railing (a and b) and road (c and d), or natural, such as stone (e and f)

Fig. 5 Two pounding substrates used in succession by a Nicobar long-tailed macaque at Campbell Bay, Great Nicobar island, India, December 2018 to March 2019. The picture on the left represents the first substrate that is selected by a male macaque to pound a coconut. This substrate is brittle and surrounded by broken pieces. Subsequently, the male switches to a smoother pounding substrate (picture on the right), that is likely more suitable for pounding the coconut.

Fig. 6 Use of a rolling substrate (i.e., a log) to process food by Nicobar long-tailed macaques at Campbell Bay, Great Nicobar island, India, December 2018 to March 2019. An adult male presses the food against the platform using his palm (a and b), and he rolls the food back and forth against the platform with his palm (c and d).

Fig. 7 Use of a stick to process food in Nicobar long-tailed macaques at Campbell Bay, Great Nicobar island, India, December 2018 to March 2019. The male macaque selects the leaf and the stick (a); he holds the stick and the leaf (b); and he processes the leaf with the help of the stick (c and d).

Fig. 8 Use of leaves by Nicobar long-tailed macaques at Campbell Bay, Great Nicobar island, India, December 2018 to March 2019, to provide a grip on a coconut (a and b), and to rub the surface of a coconut (c and d)

Fig. 9 An adult male Nicobar long-tailed macaque modifies a stick then uses it to rub/scratch his genital area at Campbell Bay, Great Nicobar island, India, December 2018 to March 2019. The male selects the stick (a); he cleans the stick by removing the leaves (b and c); and he uses the stick to scratch its genital region (d).

Fig. 10 Use of a stick as a play object among juvenile Nicobar long-tailed macaques at Campbell Bay, Great Nicobar island, India, December 2018 to March 2019, by twirling (a), holding (b), dragging (c and d), and flipping the branch (d).

Fig. 11 Use of iron rods to display aggression in Nicobar long-tailed macaques at Campbell Bay, Great Nicobar island, India, December 2018 to March 2019. In (a) individual A shakes the metal rod to threaten individual B, while in (b) individual B shakes the metal rod in response to individual A. In (c) individual B returns and sits, while individual A observes him, and in (d) individual A again returns and shakes the rods more rigorously.

579 **Tables**

580 Table 1. Summary and definitions of the contexts in which Nicobar long-tailed macaques at
581 Campbell Bay, Great Nicobar island, India, showed tool use and object manipulation
582 (December 2018 to March 2019.

583

Context	Definition	Example
Foraging	Energetic searching for food items using objects to acquire, process, manipulate and/or transport food	Scraping tool, rolling substrate
Hygiene	Use of an object to remove dust or any other unwanted particles from food	Leaves as wipers
Self-directed	Use of an object to relieve irritation on the animal's body	Sticks to self-scratch
Self-hygiene	Use of an object to clean the animal's own body	Fibre as dental groom
Play	One or more individuals use an object expressly for the purpose of entertainment	Sticks, iron roads, cloth

	Using an object to transfer information to the other members in a group	
Possible Communication	or	Resonance rod
	Use of an object to 1. threaten other individual. 2. mimic oneself as a larger or stronger individual.	

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Fig. 1 Location of the field site (© Google Earth)

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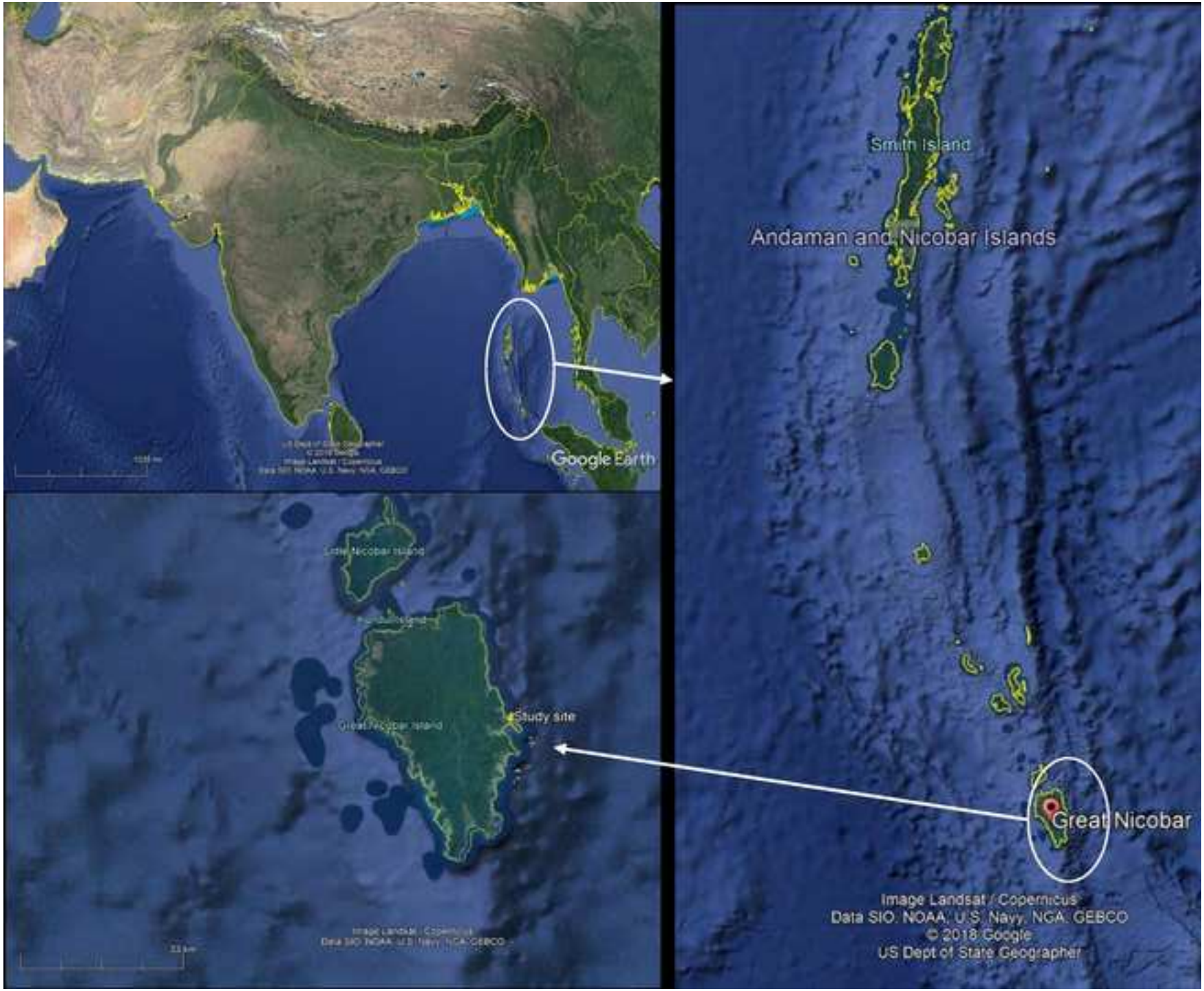
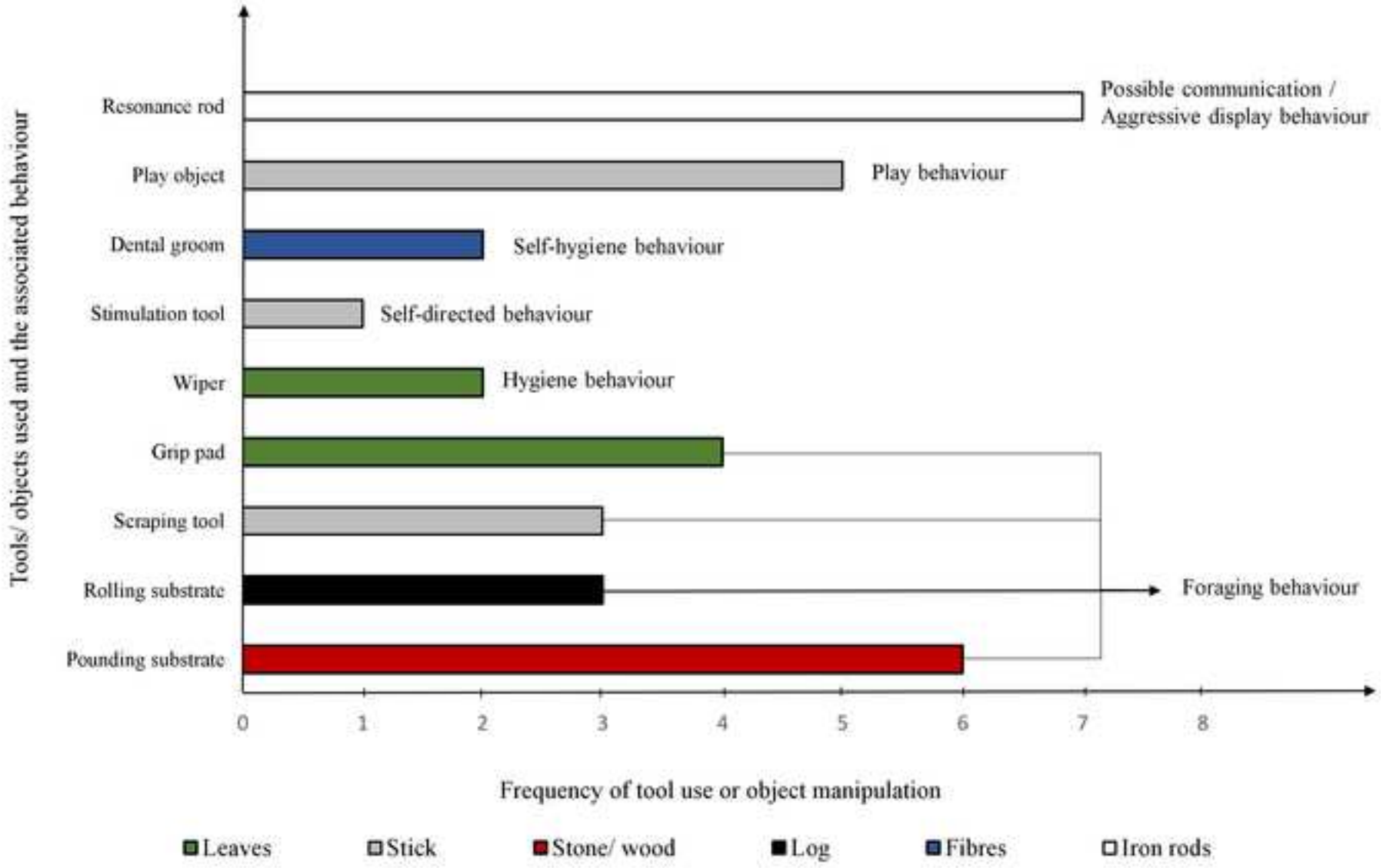


Fig. 2 Frequency of tools and objects used and associated behaviour displayed by Nicobar long-tailed macaques at Campbell Bay, Great Nicobar island, India, December



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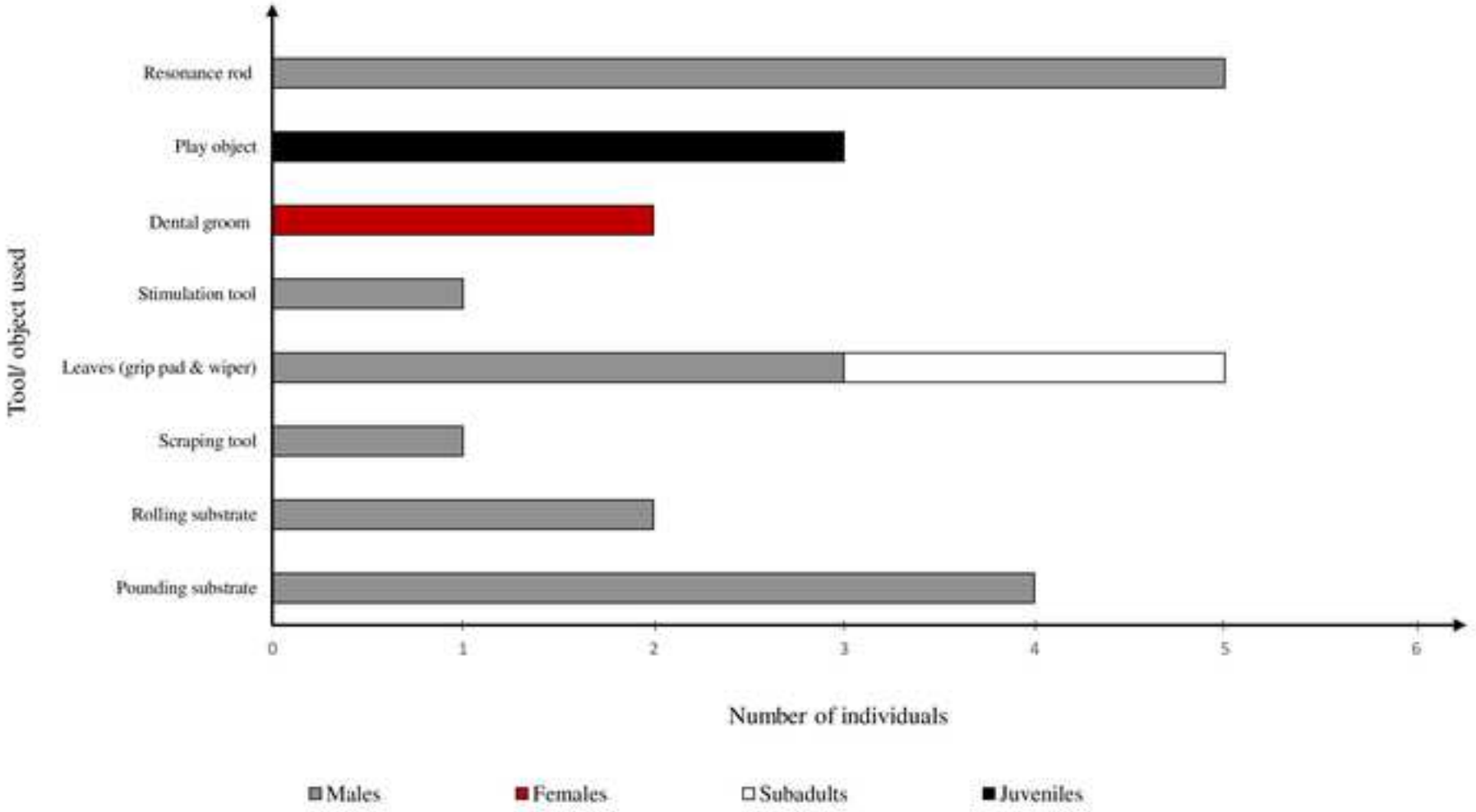

Fig. 4 Use of different pounding substrates by Nicobar long-tailed macaques at Campbell Bay, Great Nicobar island, India,

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Fig. 5 Two pounding substrates used in succession by a Nicobar long-tailed macaque at Campbell Bay, Great Nicobar island, India, December 2018 to March 2019. The

Fig. 6 Use of a rolling substrate (i.e., a log) to process food by Nicobar long-tailed macaques at Campbell Bay, Great Nicobar island, India, December 2018 to March

a

b

c

d

Fig. 7 Use of a stick to process food in Nicobar long-tailed macaques at Campbell Bay, Great Nicobar island, India, December 2018 to March 2019. The macaque selects the

a

b

c

d

Fig. 8 Use of leaves by Nicobar long-tailed macaques at Campbell Bay, Great Nicobar island, India, December 2018 to March 2019, to provide a grip on a coconut (a and b),

Fig. 9 An adult male Nicobar long-tailed macaque modifies a stick then uses it to rub/scratch his genital area at Campbell Bay, Great Nicobar island, India, December

Click here to download Figure Fig 9.jpg

Fig. 10 Use of a stick as a play object among juvenile Nicobar long-tailed macaques at Campbell Bay, Great Nicobar island,

Click here to download Figure Fig 10.jpg

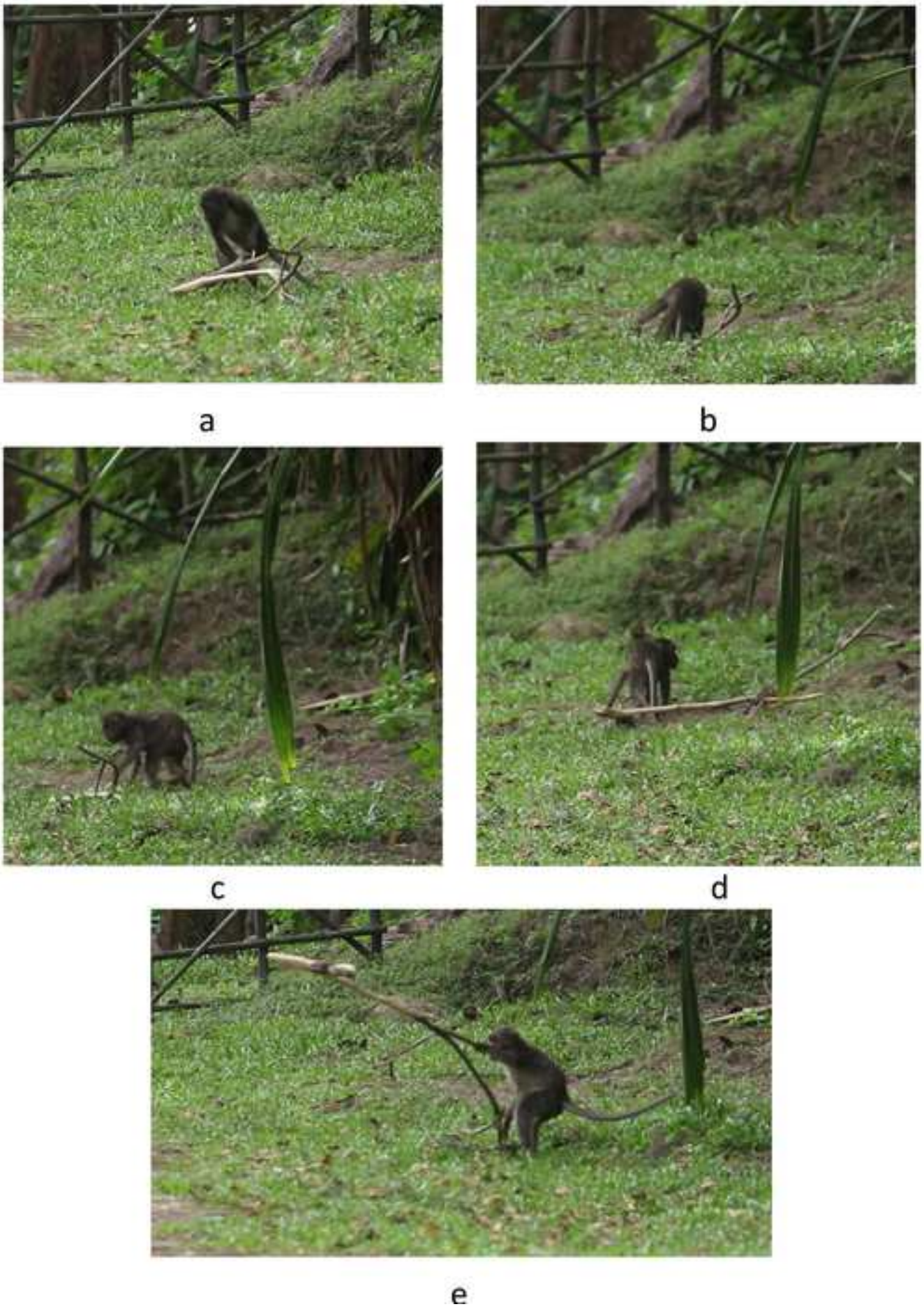

Fig. 11 Use of iron rods to display aggression in Nicobar long-tailed macaques at Campbell Bay, Great Nicobar island, India, December 2018 to March 2019. In (a)

Supplementary video

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